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THE EFFECT OF TEMPERATURE ON OVIPOSITION INTERVAL AND EARLY DEVELOPMENT IN THERIDION RUFIPES LUCAS (ARANEAE, THERIDIIDAE)

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ABSTRACT

The effect of temperature on oviposition rate and early development of *Theridion rufipes* in northern Queensland was investigated. Development did not proceed at 20° C, and embryos and postembryos responded differently to temperatures of 25° C and 30° C. The time interval between ovipositions by the female was markedly extended at 20° C, a temperature at which development was unlikely.

INTRODUCTION

Spider species for which the relationship between temperature and development has been reported include *Tegenaria atrica* (C. Koch) (Browning 1941), *Cheiracanthium inclusum* (Hentz) (Peck and Whitcomb 1970), *Thanatus striatus* (C. Koch) and *Allomengea scopigera* (Grube) (Schaefer 1977) and *Latrodectus hasselti* Thorell (Downes 1987). The present study adds *Theridion rufipes* Lucas to this list, and shows that the oviposition intervals (i.e., the time periods between the construction of egg sacs, over the iteroparous sequence) are temperaturedependent in a comparable way.

T. rufipes is widely distributed, primarily in tropical and subtropical regions, but with a range extending into temperate zones; it was first described from specimens collected in Algeria. Its original range may be hard to determine because its close association with man has probably led to extensive transportation. A recent first report (Sugarman 1979) of its occurrence in the Marshall Islands, for instance, may reflect its previous introduction by man. In the United States its range includes Texas and Florida (Levi and Randolph 1975).

MATERIALS AND METHODS

A total of 60 *T. rufipes* females was collected in Townsville, of which 51 were immature and unmated and nine were mature and had mated and produced their first egg sac in the field. These females were separated into three groups of 20 (17 immature, three mature in each case), and each group was kept at one of three experimental temperatures (20, 25 and $30^{\circ}C \pm 1^{\circ}C$). The photoperiod was in

each case 14/10 hours light/dark. After their maturation molt, the previously immature females were mated, and on those (31) occasions when mating took place directly, and the male was either then killed by the female or removed, it was possible to record the time from mating to first oviposition. Times between subsequent ovipositions of all females (lab-mated and field-mated) were routinely recorded.

Spiders were confined individually in glass tubes measuring 50×20 mm diameter, with perforated plastic stoppers. Twice weekly, each was fed an identical diet of insect prey, including *Drosophila* sp., muscoid flies and native cockroaches. Water was not provided.

Observations were normally made daily; when ovipositions, hatchings, molts or emergences coincided with missed daily inspections, these data were not included in the results. Hence, although the spiders produced 338 egg sacs, only 287 of these gave oviposition interval values and 249 provided development data at 25 and 30°C; those (45) sacs that were constructed at 20°C gave the negative results for development at that temperature. All sacs were incubated at the same temperatures at which they were constructed.

Embryonic development times were obtained from 60 egg sacs which were teased open and housed in glass cavity blocks, the glass covers of which were separated from the rims of the blocks by a layer of non-absorbent cotton wool, with a little vaseline as adherent. By pseudoreplication, 40 of these same sacs gave postembryonic development times. The time from first molt to emergence was obtained from 189 egg sacs which were transferred to fresh 50 \times 20 mm glass tubes with perforated plastic stoppers (these containers were also used for the 20°C sacs mentioned above), and kept intact until emergence occurred. The interval between the first molt and emergence was calculated by subtraction of the oviposition-first molt time (as determined from teased-open sacs) from the oviposition-emergence time of the intact sacs. Some possible inaccuracies of this procedure were considered by Downes (1987).

All developmental data are for whole broods (i.e., egg sacs) rather than for individual spiderlings. Although individuals varied in their rate of development, developmental synchrony was very close at the temperatures at which development occurred in this study. The values for the interval between oviposition and emergence of spiderlings from the egg sac were necessarily wholebrood values, so it was felt justifiable to use whole-brood means to compute corresponding values for intervals between oviposition and hatching (= embryo) and between hatching and the first molt (= postembryo). Hatch time was defined as the time of the rupture of the chorion. Field temperatures were provided by the Geography Department of James Cook University.

RESULTS

Development did not proceed at 20° C. The mean duration, at 25 and 30° C, of the embryonic, postembryonic and first instar stages within the egg sac (i.e., from oviposition to hatching, molting and emergence respectively) are given in Table 1. The temperature increase of 5°C from 25°C produced a decrease in development time of 2.7 days (28%) for the embryonic stage but only 0.3 days (14%) for the postembryonic stage.

		Duration of Develo	pmental	Stages	
evelopmental stage	20° C	25° C	cumul.	30° C	cumul.
Embryo	No devel. (45)	9.8 SE 0.18 (45)	9.8	7.1 SE 0.27 (15)	7.1
Postembryo	_	2.1 SE 0.22 (27)	11.9	1.8 SE 0.37 (13)	8.9
First instar to emergence	_	2.4 SE 0.07 (124)	14.3	3.2 SE 0.27 (65)	12.1

Table 1.—The early development of *Theridion rufipes*. Values are given as mean interval in days, with standard error and (sample size). Cumulative values (cumul.) are given as values only. Values are means of whole broods (i.e., egg sacs), not of individual spiderlings.

Despite the fact that the overall development time from oviposition to emergence decreased by 2.2 days (15%) with the same temperature change (Table 1, cumulative values), the within-sac first instar stage time actually increased by 0.8 days (33%), from 2.4 to 3.2 days (Table 1, non-cumulative values).

There was no evidence that the adult female spiders were adversely affected by the experimental temperature extremes of 20 and 30° C, except that matings were rarer at the former temperature. However, the oviposition sequence was significantly extended at 20° C. Times, in days, separating the ovipositions of the iteroparous sequence are presented in Table 2. It is unfortunate that so few (three) instances were recorded of mating-oviposition at 20° C because the mean of these few values is by far the highest of those presented. The time between mating and the first oviposition is much shorter than that between subsequent ovipositions at temperatures that favor normal early development, but the data of Table 2 suggest that the reverse may be true at a temperature at which development is not assured.

DISCUSSION

As in all poikilotherms, temperature is usually the most critical environmental factor influencing the rate of development. However, an animal rarely develops under a constant unchanging temperature regime but rather experiences daily temperature variation around a gradually changing seasonal mean. *Latrodectus hasselti*, for example, commonly experiences temperatures of 30°C or greater in Townsville, but 30°C is close to an upper limit of temperature tolerance if applied continuously (Downes 1987).

The relative duration of the three pre-emergence phases of *T. rufipes* (embryo, postembryo and the first instar (part)) alters with the temperature change. The embryonic period takes up 69% of the total time to emergence at 25°C but only 59% of the total time at 30°C. The relative duration of the much shorter

Table 2.—The effect of temperature on time from mating to first oviposition and between subsequent ovipositions in *Theridion rufipes*. Values are given as mean interval in days, with standard error and (sample size).

Temperature (°C)	Mating to first oviposition	Subsequent oviposition intervals
20	47.7 SE 0.37 (3)	26.2 SE 2.16 (38)
25	6.6 SE 1.03 (17)	16.1 SE 0.57 (123)
30	6.3 SE 1.08 (11)	14.1 SE 0.61 (95)

postembryonic period remains unaltered (15% of the total time), while the relative (and indeed the absolute) time from the first ecdysis to emergence increases from 17% at 25°C to 26% at 30°C. This does not in itself imply any difference in the physiological response to temperature between embryos and postembryos, or between embryos and first instar spiderlings; it may be that the first instar spiderlings respond to high temperatures by remaining in the egg sac. This would be advantageous because the spiderlings would desiccate more rapidly once out of the cocoon owing to their increased exposure and increased activity. If this is so, moderately high temperatures may prolong the time spent in the egg sac by the first instars; this would explain the apparent increase in development time of the first instars in Table 1. In fact this phase is not a developmental stage in the same sense as the two earlier stages; the period from first to second ecdysis, rather than that from first ecdysis to emergence, would be more comparable.

It is not clear why the embryo and postembryo stages respond differently to a temperature decrease of 5° C from 30° C, the embryo stage increasing its development time by 38% (2.7 days) and the postembryo stage by only 17% (0.3 days). These differences may relate to the (unknown) overwintering strategy of this species in temperate zones. A 'stronger' response from embryos than from postembryos suggests physiological affinities with populations that undergo egg overwintering, but most spider species do not overwinter in the egg stage, according to Foelix (1982).

In temperate regions *T. rufipes* may be found to develop (slower) at temperatures down to 10° C or below, as does *Latrodectus hasselti* from temperate zones (Forster 1984). Why this does not occur in tropical populations is an open question, but over the past six years the mean monthly temperature in this district of Townsville has fallen below 19°C only in one two-month period, when it sank to 18.3°C (June and July 1982). Minimum temperatures do occasionally go below 10°C during some nights of the cooler dry season, but corresponding day temperatures on these occasions are likely to be in excess of 20° C.

A temperature cycle of $15-25^{\circ}$ C, evenly changing over a 24-hour period, may produce a very different outcome from a constant 20° C regime, despite the former's mean value of 20° C.

In view of the curtailment of development at 20° C, the data of Table 2 suggest that there may be a behavioral response on the part of *T. rufipes* females, delaying the production of egg sacs at temperatures at which development is unlikely. In a poikilotherm such as *T. rufipes* physiological processes such as öogenesis will be subject to the effects of temperature just as surely as will embryonic development, but it would be interesting if it could be demonstrated that oviposition behavior responds more strongly than physiological/metabolic processes, to a fall in temperature of 5°C from 25 to 20°C. Such an investigation was beyond the scope of the present study.

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